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THE RELATIONSHIP BETWEEN CALCIUM GLAND SIZE, FECUNDITY AND SOCIAL BEHAVIOR IN THE UNISEXUAL GECKOS, *LEPIDODACTYLUS LUGUBRIS* AND *HEMIDACTYLUS GARNOTII*

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ABSTRACT: The three present experiments examined the relationship between calcium gland size, fecundity, and dominance/social behavior in the unisexual geckos, *Lepidodactylus lugubris* and *Hemidactylus garnotii*. Study 1 examined the above variables while the geckos were housed communally and solitarily. *L. lugubris* established stable dominance hierarchies through aggressive interactions, whereas *H. garnotii* neither established a dominance hierarchy nor displayed signs of aggression while housed communally. Eggs were developed by 4 of 4 dominant *L. lugubris* but by only 1 of 4 subordinate *L. lugubris* and 1 of 6 *H. garnotii*. Calcium glands decreased in size in the subordinate *L. lugubris* and *H. garnotii* during communal housing, then recovered when the geckos were housed solitarily. Study 2 examined the relationship between reproductive state and calcium gland size in *L. lugubris*. Calcium glands were found to be smallest prior to and immediately after oviposition and largest when eggs were yolking follicles. Study 3 examined the effect of sociality on fecundity in *H. garnotii*. Egg development was not related to whether geckos were housed solitarily or as dyads. Calcium gland size in geckos appears to be related to both stress and to the reproductive state of the gecko. We hypothesize that stress decreases the size of geckos' calcium glands resulting in decreased egg production in stressed animals.

Subordinates usually produce fewer offspring than dominants when species form strict dominance hierarchies (for example, primates, Abbot, 1987; birds, Ekman, 1987; reptiles, Brown & Sakai, 1988). Being a subordinate in a dominance hierarchy is stressful to an animal (Chapais

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& Schulman, 1983). Brown and Sakai (1988) found that the unisexual gecko, *Lepidodactylus lugubris*, formed stable dominance hierarchies in captivity and that fewer eggs were developed by subordinates when geckos were housed as quadrads. Further research on *L. lugubris* found that calcium gland size was also related to dominance rank (Brown et al., 1991). Subordinate geckos had smaller calcium glands than dominant geckos. The subordinates' calcium glands, however, increased in size after the geckos were housed solitarily. Research has shown that heat stress is related to decreased ionized calcium blood levels in chickens resulting in detrimental egg shell formation (Odom et al., 1986). Additionally symptoms of porcine stress syndrome are correlated with inefficient calcium storage in muscle mitochondria in pigs (Cheah & Cheah, 1979). Therefore the stress experienced by subordinate geckos may be affecting the availability of calcium and/or the storage ability of their calcium glands.

Calcium glands are found only in subfamilies of geckos that lay calcareous shelled eggs (Bustard, 1968). Ineich and Gardner (1989) found that calcium glands varied in size relative to the females' reproductive states. When Ineich and Gardner dissected geckos, they found that *L. lugubris* with small to moderately sized calcium glands were in an early stage of egg development, while geckos with larger glands had larger eggs. It was also observed that the glands varied in size just prior to egg laying. The variance in calcium gland size was believed to be associated with the timing of calcium deposition onto the eggs.

Little is known about the sociality of the unisexual gecko, *Hemidactylus garnotii*, and how the size of its calcium glands might be related to its social and reproductive states. Frankenberg (1982) reported little aggressive behavior between *H. garnotii* individuals. *H. garnotii* did not appear to form dominance hierarchies because, when one gecko moved into the vicinity of a second gecko, the first gecko always retreated.

To further our knowledge of the reproductive behavior of these two unisexual gecko species, the present study examined (1) relationships between calcium gland size, egg development and the social behavior of *H. garnotii* and *L. lugubris* geckos; (2) the relationship between reproductive state and calcium gland size in *L. lugubris*; and (3) the effects of sociality on fecundity and calcium gland size in *H. garnotii*.

METHODS

Housing Conditions

All geckos were provided with fruit flies and meal worms ad libitum. The enclosures were misted with water daily to maintain a moist and humid environment. The floor of each enclosure was covered with approximately 2 cm of pebbles. A small wooden platform was constructed so that a 2 cm crack was formed between the top and bottom layers. The platform and a piece of bark provided daytime hiding places. Timed lights were used to maintain a 12-hour light/dark cycle.

Procedure

Study 1. The geckos were obtained from Wailoa Park, Hilo, Hawaii on 2/27/94. Three different species of geckos were collected, *L. lugubris* (n = 8), *H. garnotii* (n = 6), and *Hemiphyllodactylus typus* (n = 2). Measurements of their snout-vent lengths, calcium glands, and eggs were recorded within 24 hr of capture. Eggs and calcium glands were measured by placing the gecko in a narrow plexiglas box and examining the gecko's translucent ventral surface. Eggs greater than 1 mm in size and swollen calcium glands can be observed in this manner. The width and length of each calcium gland were measured, and the areas of both glands (right and left sides) were added together for a gecko's total calcium gland size. Each gecko was marked with non-toxic paint for identification and randomly placed with three other geckos in an aquarium (51 x 28 x 31 cm). *L. lugubris* were housed in Cages 1 and 2, and *H. garnotii* in Cage 3. Cage 4 was shared by two *H. garnotii* and two *H. typus*. *H. garnotii* are rare in Hawaii, and we failed to capture eight. Geckos were kept in the communal enclosures for 28 days. A ten minute serial record of the geckos' behavior was obtained five times per week (total observation time per cage = 3.2 hr). Observations were used to determine the dominance rank of each gecko. Dominance rank was calculated by dividing the number of times a gecko won an interaction (the interaction ended with other gecko moving away) by the total number of interactions in which the gecko participated.

After 28 days in the communal aquaria, the geckos were transferred to singleton plexiglas enclosures (32 x 18 x 23 cm) for an additional 28 days. Measurements of the geckos' calcium glands and egg size were recorded once a week during both communal and solitary housing conditions. A two-part experiment was performed.

Study 2. To examine the relationship between egg development and calcium gland size in more detail, 10 *L. lugubris* were studied. Measurements of the geckos' calcium glands were taken immediately after egg laying and weekly thereafter until a second egg clutch was laid. Calcium gland size was compared for the following reproductive periods: (1) immediately after egg laying, (2) when eggs were first observed in the geckos ($MN_{egg\ size}$ = 2.6, range: 1 - 5 mm; most likely ovarian follicles), (3) the week after eggs were first observed ($MN_{egg\ size}$ = 4.4 mm, range: 3 -6 mm; most likely ovarian follicles) (4) two weeks before the second clutch was laid ($MN_{egg\ size}$ = 6.7 mm, range: 6 - 8 mm; most likely oviductal eggs) and (5) the week before the second clutch was laid ($MN_{egg\ size}$ = 8.3 mm, range: 7 - 10 mm; most likely oviductal eggs: see Jones et al. 1979 for information on ovarian vs oviductal eggs).

Study 3.   Because *H. garnotii* seemed more communally tolerant than *L. lugubris* in Study 1 and because other researchers (Crews & Fitzgerald, 1980) have proposed that some social behaviors, for example pseudocopulations, influence fecundity in unisexual lizards, we designed a study to examine sociality and its effect on fecundity in *H. garnotii*. Nine geckos with no signs of egg development were housed as dyads for 112 days and solitarily for 112 days (a tenth gecko whose data are not reported was used as a stimulus gecko for one gecko; we could not originally capture 10 *H. garnotii*).   Geckos were housed in plexiglas enclosures (32 x 18 x 23 cm) with one platform. Housing conditions were counterbalanced across geckos, 4 received the communal treatment first (June - September, 1994), 5 the solitary treatment first. Geckos then received the counterbalanced treatment (September, 1994 - January, 1995;). Geckos were randomly assigned to initial housing conditions. None of the geckos had visible signs of egg development when they received the first half of the treatment. If geckos had observable eggs at the end of the first half of the study, their placement in the second half was delayed until oviposition.

Geckos were examined each month for signs of egg development and their eggs and calcium glands were measured unless they were shedding. Data on platform use were systematically obtained across the study. Eighty-six observations were obtained in the first 112 days and 90 observations in the last 112 days of the study.

RESULTS

Study 1

Twenty-four aggressive interactions were observed between *L. lugubris* geckos housed in Cage 1 and 23 aggressive interactions between geckos in Cage 2. In contrast, no aggression was observed in the cages housing *H. garnotii* and *H. typus* geckos. Dominance hierarchies were therefore calculated only for *L. lugubris* geckos. Dominance was not significantly related to the snout-vent lengths of the geckos. For example, in Cage 1 the largest gecko was the beta animal
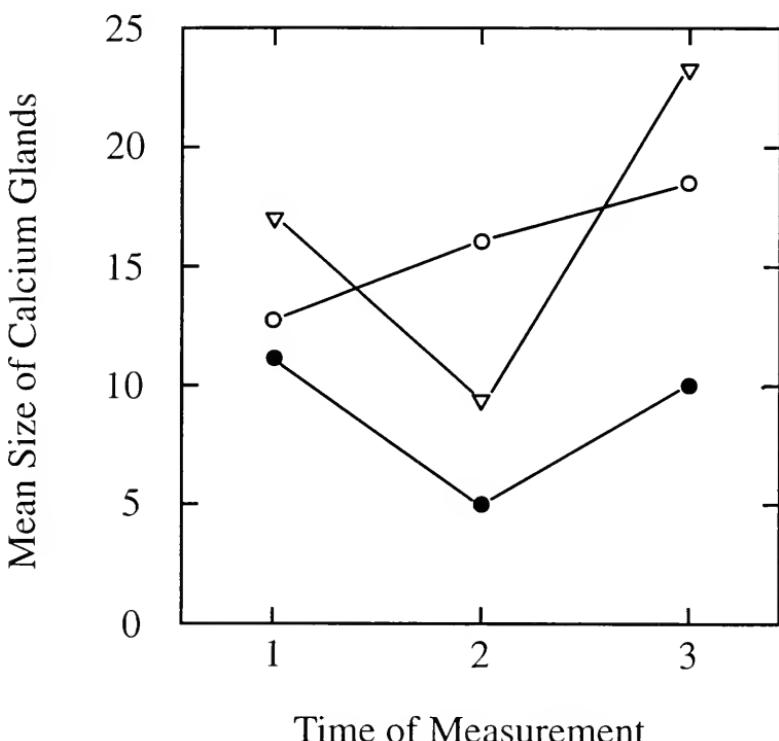
Figure 1. Size of the geckos' calcium glands in mm. The glands were measured (1) within 24 hr of the gecko's capture (2) after the geckos were housed communally for 28 days, and (3) after the geckos were housed solitarily for 28 days. The open circles represent dominant *L. lugubris* (S.D.s for dominant geckos at the 3 measure-ment times are 1.5 mm, 8.1 mm and 14.4 mm), the filled circles subordinate *L. lugubris* (S.D.s are 3.7 mm, 4.6 mm and 2.2 mm), and the open triangles *H. Garnotii* (S.D.s are 9.5 mm, 6.4 mm and 15.6 mm).

(44 mm); the alpha was 40 mm. In Cage 2 the largest gecko was the alpha (44 mm), but the second largest gecko (43 mm) was the most subordinate having 2 geckos measuring 40 mm dominant to it. Brown et al. (1991) also failed to find a relationship between size and dominance in *L. lugubris*.

Calcium gland size of dominant *L. lugubris* remained relatively stable throughout the course of the study. In contrast, calcium gland size of the subordinate *L. lugubris* and of the *H. garnotii* decreased during the time the geckos were housed communally but later increased after the geckos were housed alone (see Figure 1). All of the dominant (2 most dominant geckos in each cage) *L. lugubris* (4/4) developed eggs during the study while only one subordinate L. lugubris (1/4) and one *H. garnotii* (1/6) developed eggs.

The time the geckos were observed in proximity (less than 3 cm apart, for 2 to 10 min) in the platform or under the bark without displaying aggressive behavior was compared across the species. *H. garnotii* geckos spent significantly more time in proximity (7.4 min/10 min) than the *L. lugubris* (1.4 min/10 min), $\underline{F}$ (1,13) = 69.7; N = 14; p < .01. *H. garnotii* housed in Cage 3 were observed in proximity in 9 dyads, in 11 triads, and 2 quadrads. Cage 4 *H. garnotii* were observed in proximity in 18 dyads, in 3 triads, and once in a quadrad.

Study 2

Geckos' calcium glands were smallest prior to and immediately after oviposition. The glands were largest the week that eggs were first observed in the geckos and remained large through the week before oviposition (Figure 2). The overall difference between calcium gland size across the geckos' reproductive states was significant, $F(4, 36) = 4.29$; p < .01. As can be observed in Figure 2, the mean calcium gland size immediately after laying and the week before the second clutch was laid are equal. Subsequent tests (Neuman-Keuls) found that calcium gland size at the above two reproductive periods differed significantly from the gland measurement when the eggs were first observed (p < .05) and the week after eggs were first observed (p < .05). Other pair-wise comparisons were nonsignificant. Although increases in calcium gland size were observed in 9/10 geckos, one gecko developed and laid eggs without visible signs of calcium glands.
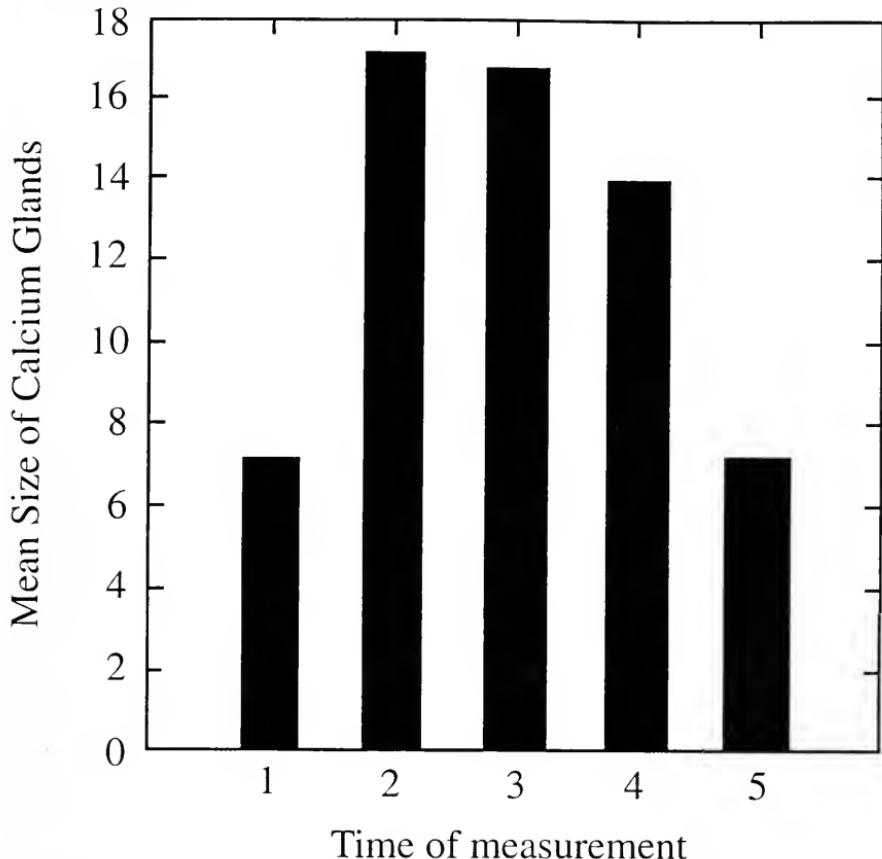
Figure 2. Size of the geckos' calcium glands by reproductive periods: (1) immediately after egg laying (SD = 10.3), (2) when eggs were first observed in the geckos (SD = 14.0), (3) the week subsequent to first egg observation (SD = 11.9), (4) two weeks before the second egg clutch was laid (SD = 13.8), and (5) the week before the second clutch was laid (SD = 9.4).

Study 3

The geckos were more likely to be in the platform when observations were made with the lights on (M(proportion of time in platform) = .89) than when the lights were off (M(proportion of time in platform) = .31). A highly significant difference was found, $F(1,8) = 109.84$; $p < .0001$. Similar data were obtained during the second half of the study (M(lights on) = .82; M(lights off) = .03). Therefore subsequent analyses on time observed in the platform were conducted only when the data were obtained with the lights on.

H. garnotii geckos spent a significantly greater percentage of time in the platform when they were housed solitarily (M = .93) than when they were housed as dyads (M = .79), $F(1,8) = 10.34$; $p < .02$. When geckos were housed as dyads, the geckos were observed together in the platform in 63% of the observations (range: 36% - 96%).   There was no difference in egg development and laying between the solitary (3/9) and the dyadic (3/9) conditions. Additionally the average size of the geckos' calcium glands did not significantly differ between the solitary (M = 9.56; s = 8.06) and the dyadic (M = 7.13; s = 8.4) conditions, $F(1,8) = 1.66$; $p > .05$.

DISCUSSION

The *L. lugubris* geckos in the present study formed strict dominance hierarchies in which the subordinate geckos developed fewer eggs than the dominants. These findings replicated our previous results (Brown & O'Brien, 1993) and the findings of other studies on unisexual lizards (Grassman & Crews, 1987). We found that calcium gland size was not only related to the gecko's position in the dominance hierarchy but also to the phase of the gecko's reproductive cycle. Dominant geckos and those geckos with yolking follicles possessed the largest calcium glands. We hypothesize that the decreased egg development observed in subordinate *L. lugubris* was related to the small size of their calcium glands. The pathway we propose is that subordination is stressful, stress causes the gecko to experience decreased levels of available calcium, and decreased calcium levels result in decreased egg production. This process is modulated by the reproductive cycle of the gecko.

The *H. garnotii* geckos in Study 1 resembled the subordinate more than the dominant *L. lugubris* in terms of egg production and calcium gland size. Additionally, Study 3 found that the *H. garnotii* produced few egg clutches regardless of their housing conditions. Meshaka (1994) proposed that *H. garnotii* should produce an egg clutch every three months; therefore in Study 3 the *H. garnotii* should have produced 18 clutches rather than the 6 observed.   The calcium glands of the *H. garnotii* in Study 3 were also the same size as the communally housed geckos in Study 1. Some reptiles are extremely stressed by captivity (Cowan, 1980). It may be that the long-term captivity experienced by the *H. garnotii* in Study 3 produced stressed animals and subsequently stressed behaviors. The stress of captivity was most likely responsible for the *H. garnotii's* decreased calcium gland size and egg production paralleling the stress of subordination in *L. lugubris*. If captivity is

indeed stressful for *H. garnotii*, the fact that the same number of geckos produced egg clutches in dyadic and solitary conditions in Study 3 cannot answer the question of whether or not *H. garnotii's* fecundity is increased by pseudosexual behavior as has been proposed for whiptail lizards (Crews & Fitzgerald, 1980).

In the present studies *H. garnotii* geckos were not observed defending personal space as reported by Frankenberg (1982) for a Florida population. The fact that several clones of *H. garnotii* (Moritz et al., 1993) exist suggests that the Hawaii and Florida populations might have been founded by different females from different clones and therefore display behavioral differences.

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VARIATIONS IN THE STRUCTURE OF THE PEEP VOCALIZATION OF FEMALE DOMESTIC CHICKS (*GALLUS GALLUS DOMESTICUS*) ON DAYS FIVE AND SIX POST-HATCHING

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ABSTRACT: Domestic chicks (*Gallus gallus domesticus*) were reared in pairs from day three post-hatching. On the fifth day of life, a chick was separated from its brood mate and 30 secs. later the chicks' vocalizations were recorded for five minutes. The recordings were analysed using Canary 1.1 sound analysis system running on Mac II vx. Seven acoustic parameters of the peep vocalizations of female chicks were measured (duration (msec), maximum frequency (kHz), minimum frequency (kHz), difference between maximum and minimum frequency (kHz), peak frequency (kHz), energy (watts) and average power (joules)). During separation chicks produced peep calls that differed in structure. In total, 12 female chicks' vocalizations were examined and seven chicks produced three distinct peeps . These were classified as short, medium and long. Three calls of each type for each chick were examined. Short peeps have a narrow frequency range and short duration, medium peeps have a wider frequency range, longer duration and a short upper inversion preceding the descending frequency. Long peeps have the widest frequency range, the longest duration and have the most complex structure. The main finding of this study is that the chick of the domestic fowl can produce three distinct types of peep call.

Adult domestic fowl (*Gallus gallus domesticus*) produce approximately 24 different vocalizations (Collias, 1987). The chick of the domestic fowl produces two main vocalizations: twitters (pleasure notes) and peeps (distress calls). They also produce the waning bout (Andrew, 1963), shriek (fear note), trill (fear trill) (Andrew, 1964; Collias and Joos, 1953) and the pleasure trill (Collias, 1987). Twitters

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swing upwards in pitch while peeps are characterised by a single descending frequency limb (Andrew, 1963, 1964; Collias, 1987; Collias and Joos, 1953).

Wood-Gush (1971) reviewed several studies using spectrogram analysis of chick vocalizations and pointed out that it is not always clear which calls (as described by different authors) are the same. Different names can be given to the same call and the same name can be given to calls that differ in structure. For example the 'Le cri d'appel du Poussin isolé' of Guyomarc'h (1962), the distress call of Collias and Joos (1953) and the peeps of Andrew (1964) are classified by Wood-Gush (1971, p. 28-29) as being the same call, yet he points out that the spectrograms presented by these researchers show differences in structure. 'Le cri d'appel de Poussin isolé' has a wider frequency range than the other peep calls and a more complex structure, the distress call of Collias and Joos (1953)and the peep of Andrew (1964) both have an intermediate and short frequency ranges, the structure of the calls is not as complex as that of the call of Guyomarc'h. Wood-Gush (1971) emphasised the need for a more objective and detailed description of the calls and of the stimulus situation in which they occur. Apart from a detailed sonograph-based analysis of the maternal calls of the broody hen (Kent, 1989, 1993), little attention has been given to a detailed analysis of the structure, or development of vocalizations in the domestic fowl.

The purpose of this paper is to examine in detail three different types of peep vocalization of the five to six day-old domestic chick. At this age the distance between the broody hen and her chicks in the natural environment increases sharply (Workman and Andrew, 1989) and their vocal interactions (Evans, 1975) become more important. Further, it has been shown that following separation from a companion, chicks produced more peeps on day 7 than on day 3 post-hatching (Kaufman and Hinde, 1961).

METHOD

Subjects

Sixteen brown leghorn chicks from two batches of eggs (Batch A: 1 male, 3 females; Batch B: 3 males, 9 females) were reared in pairs from day 3 post-hatching. The four males were eliminated from the statistical analysis. Thus, 12 female chicks were used.

Procedure

From hatching to day three post-hatching, chicks were group reared with their hatch mates. Then they were randomly selected and placed in pairs in wooden rearing pens (59 cm x 60 cm x 44 cm high) with a wire mesh roof, and a front door that slid upwards. The floor of each pen was covered with chopped straw, food and water was available at all times. The rearing pens were maintained in a house (488 cm x 423 cm) with a 250 watt infra red heating light suspended above each rearing pen. Each chick had an individually coloured leg ring.

Testing began on the fifth day post-hatching (48 hrs. after being placed in the rearing pen). A pair of chicks in their rearing pen was first moved to a wood panelled room, with a 250 watt infra red light positioned over the pen to maintain temperature stability. The chicks were then removed from the rearing pen and placed in a covered holding box for 5 minutes. The holding box was removed from the testing room to ensure that the chicks were out of each others hearing range while recording took place. One of the chicks was then returned to the rearing pen and 30 seconds later a 5 minute recording session began using an ITT SL 520 tape recorder and VIVANCO unidirectional microphone suspended approximately 10 cm above the roof of the box. Following the test period the chick was placed back in the holding box for five minutes after which, the second chick was tested. This procedure was repeated on day six with the testing order reversed. With Batch B the procedure was slightly different with one chick being removed from the rearing pen and 30 seconds later the 5 minute recording session began with the remaining chick. Following recording the two chicks were placed back in the rearing pen for five minutes and the procedure was repeated with the second chick being recorded. This procedure was repeated on day six with the testing order reversed. An observer was situated behind a wooden screen with a 5 cm x 26 cm slot which allowed observation of the chicks with minimal interference.

Measures

The taped recordings of the peeps vocalizations were transferred to a Mac II vx computer and analysed using the Canary 1.1 sound analysis program (The Cornell Bioacoustics Workstation) (Charif et al. 1993; for review see Wilkinson, 1994). All spectrograms were analysed with a filter bandwidth set at 352.94 Hz (see Fig. 1).
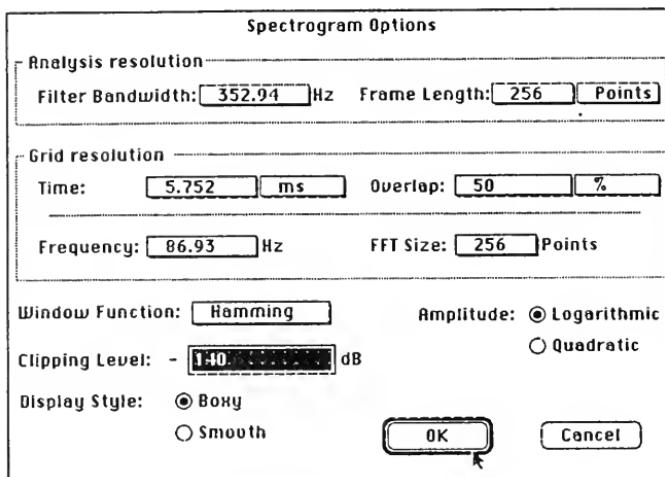
Figure 1. The Canary 1.1 spectrogram options window as used in this study.

Seven chicks produced three peep type calls (short, medium and long) and these calls resemble the calls reviewed by Wood-Gush (1971). The following seven parameters were measured for each of the three peeps recorded:

1. Duration (msec.)
2. Maximum Frequency (kHz)
3. Minimum Frequency (kHz)
4. Difference between Max. and Min Frequency (kHz)
5. Peak Frequency (kHz)
6. Energy (watts)
7. Average Power (joules)

Parameters [1-5] describe the structure of the call. Peak frequency refers to the frequency with the highest amplitude. Parameters 6 and 7 give details of energy use. The latter two parameters were controlled for by having the microphone in fixed suspension above the centre of the pen, reducing the need to have the chick facing in any one direction during testing. The rate of calling was also examined. Measurement of the seven parameters was possible by selecting the entire call, then holding down the command key and clicking the mouse button. This logged all measurements to Canary datalog window for further analysis. Seven chicks produced the three calls types, and three examples of each call type were analysed.

Statistical Procedures

The data for each of the three call types of each chick were averaged and analysed using a two way ANOVA, Scheffe's method, (Edwards, 1972), and t-tests. As it was not possible to capture the highest frequencies of the long peeps for any of the chicks due to software constraints, a nominal maximum frequency of 11.1 kHz was assigned as the maximum frequency for the long calls. A t-test was used to compare the short and medium peeps for the parameters of maximum frequency and difference between maximum and minimum frequencies. The loss of information on the long peep for energy and average power is minimal as the values for the peak frequency (see Table 1) indicates that the maximum values for energy and power to be well below the nominal maximum range of 11.1 kHz. Therefore, statistical comparisons were applied to these and the other parameters.

The cassette tapes of the seven chicks used in the statistical analysis were further examined to see if call types could be considered discrete or part of a continuum. The taped recordings were examined using SoundEdit Pro 1.0 on a Mac II vx. This enabled investigation of the tapes in 30 second sections. As the three call types were acoustically distinct it was possible to determine where calls changed from one call type to another. Waveforms and power spectrums were produced for the change over points and saved in SoundEdit format, a file format readable by Canary 1.1. This allowed the production of spectrograms of these call for a more detailed analysis.

RESULTS

A description of the peep call

The peep calls were identified first by an aural inspection of the tapes and then by a visual inspection of the spectrograms. This method is similar to that used by Seyfarth, Cheney and Marler (1980) with three different vervet monkey alarm calls. Classification of the calls was facilitated by their occurrence in bouts of calls with the same structure. Andrew defined a bout as "a group of calls, separated from each other by intervals of .20 sec. or less" (1963, p. 934).

The peep call is characterized by descending frequencies. Seven of the 12 chicks produced three distinct peep types that are classified
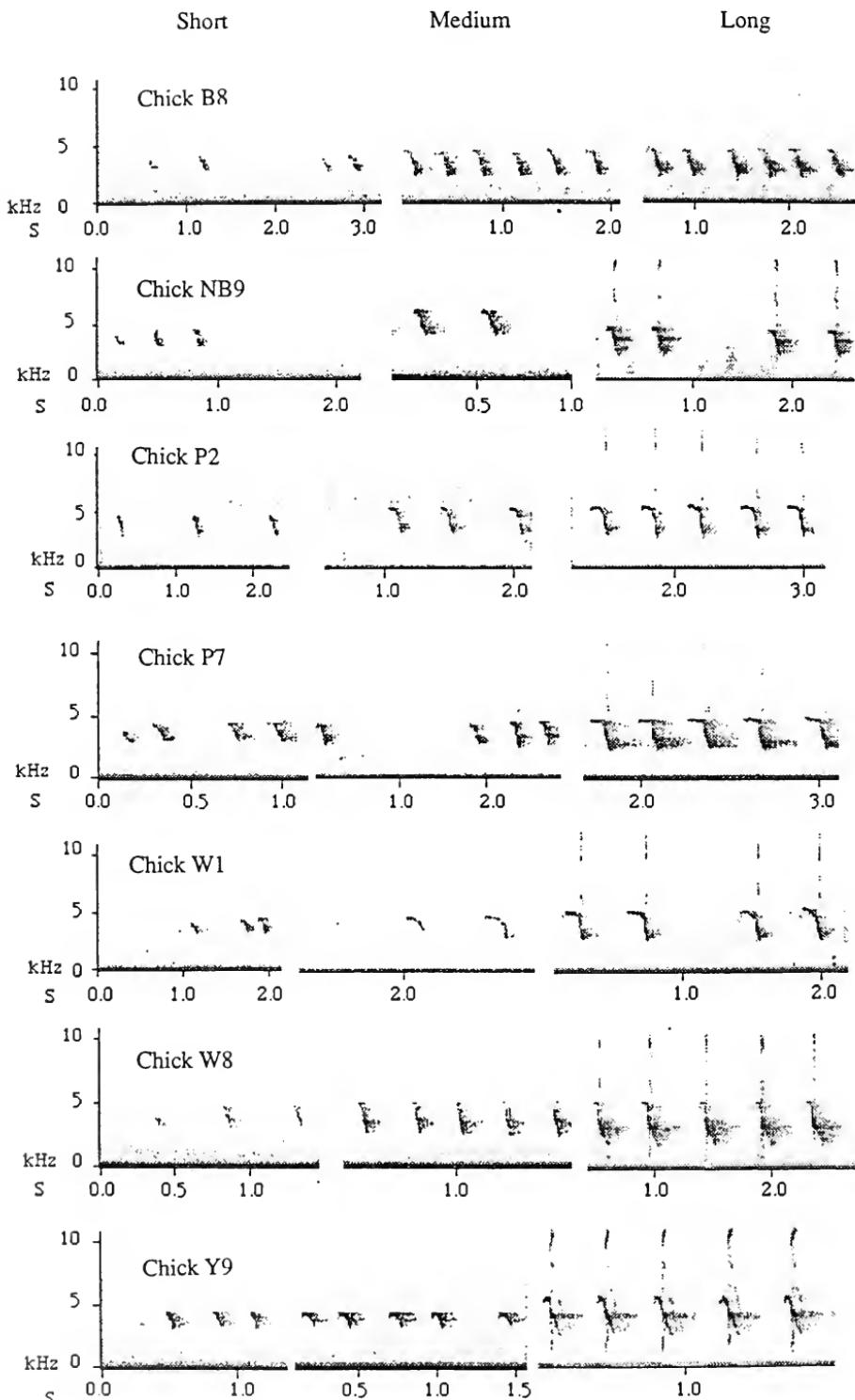
Figure 2. On the previous page are shown spectrograms of the short peep (left column), medium peep (middle column) and long peep (right column) emitted by the seven chicks on days 5-6 post-hatching. The identity of each chick is located in the upper left hand corner above the short call.

here as short, medium and long peeps and are the subject of statistical analysis. Of the remaining five chicks, three emitted medium and long peeps and two other chicks emitted long peeps only. The short peep was short in duration and had a relatively narrow frequency (kHz) range when compared to the medium calls. The short peep had a single descending frequency slope and has the least complex structure. The medium peep had a greater frequency range (kHz) and a short upper inversion indicating that the medium peep contains an ascending element that was not present in the short peep. The long peep had the most complex structure which occupied a wider frequency range than either the short or medium peeps. The upper inversion present in the medium peep is also present in the long peep and is more evident (Figure 2).

Parameter analysis

The long peep is, as its name implies is longer in duration than either the medium or short peep and it also has a greater maximum frequency, lower minimum frequency and has greater power and energy than either the medium or short peeps (Table 1). Further, for the parameters of duration and peak frequency, the coefficient of variation (c.v.) becomes lower as the peeps increase in length. This indicates that the long peep is a more stable form of peeping. However, for the peak frequency there is a remarkable similarity between the short, medium and long peeps (means = 3.5973 kHz, 3.2082 kHz, 3.4568 kHz respectively) and a low C.V. The minimum frequency on the other hand, has an increase in variation as the calls lengthen.

A two-way ANOVA showed a significant difference between calls (short, medium and long) for duration, minimum frequency, energy, average power. No significant differences between chicks were found except for average power (Table 2 (a)). A significant difference was found between short and medium peeps for the difference between maximum and minimum frequencies (see Table 2 (b)).

Table 1. Mean, Range, S.D., Coefficient of Variation (C.V.) of seven physical parameters for the three peep vocalizations (n=7 chicks). Three peeps for each call type for each chick were used. C.V. is not included for maximum frequency and difference between max. and min. frequencies, as true measures of these parameters are not available.

Parameters	Call Type	Mean	Range	S.D.	C.V.
Duration (ms)	Short Peep	146.9	61.8 - 213.5	53.9	36.7
	Med. Peep	240.7	183.8 - 314.4	49.5	20.6
	Long Peep	325.9	283.1 - 382.5	37.2	11.4
Maximum freq. (kHz)	Short Peep	4.3	3.2 - 3.7	0.4	8.1
	Med. Peep	4.9	4.5 - 6.1	0.3	11.6
	Long Peep	11.1	11.1 - 11.1		0.0
Minimum freq. (kHz)	Short Peep	2.9	2.6 - 3.2	0.2	6.3
	Med. Peep	2.5	2.2 - 3	0.7	9.9
	Long Peep	0.7	0 - 2.7	1.2	172.0
Difference between	Short Peep	1.4	0.8 - 1.9	0.3	23.6
max. and min.	Med. Peep	2.4	1.7 - 3.6	0.6	28.4
frequencies (kHz)	Long Peep	10.4	8.4 - 11.1		
Peak frequency (kHz)	Short Peep	3.6	3.2 - 4.4	0.4	12.3
	Med. Peep	3.2	2.7 - 4.1	0.5	16.1
	Long Peep	3.6	3.1 - 4	0.3	9.8
Energy (Watts)	Short Peep	8.0	1.9 - 20	6.6	82.7
	Med. Peep	20.7	9.3 - 51.4	14.1	67.9
	Long Peep	81.0	53.8 - 99.1	15.5	19.1
Average Power	Short Peep	1.3	0.2 - 2.5	1.0	76.3
(Joules)	Med. Peep	4.8	3 - 10	2.5	51.6
	Long Peep	27.2	16.2 - 37	7.1	26.2

Table 2(a). Two-way repeated ANOVA for five parameters on the three Peep vocalizations, short, medium and long (n=7 chicks).

Parameters	Chicks		Calls	
	F	P	F	P
Duration	1.2	NS	26.7	P<.005
Minimum frequency (kHz)	1.2	NS	20.1	P<.005
Peak frequency (kHz)	1.9	NS	1.8	NS
Energy (Watts)	1.3	NS	78.2	P<.005
Average Power (Joules)	3.05	P<.05	111.9	P<.005

Table 2(b). T-test for short versus medium mean peep vocalisations (n=7 chicks).

Parameters	Short Peep	Medium Peep	T	P
Maximum frequency (kHz)	4.3	4.9	0.5	NS
Difference between max. and min. freq. (kHz)	1.4	2.4	3.4	P<.01

The difference between the short, medium and long peeps for the parameters of duration, minimum frequency, energy and average power were examined using Scheffe's method (Edwards, 1972) (Table 3). A significant difference in duration (ms) was found between all three call types. For the parameters of minimum frequency, energy and average power a significant difference between short and long and between medium and long peeps were found.

Table 3. Multiple Comparisons using Scheffe's Method (Edwards, 1972)

Parameters	Comparison	F	P
Duration (ms)	Short v Med. Peeps	14.6	P<.01
	Short v Long Peeps	53.3	P<.005
	Med. v Long Peeps	12.0	P<.005
Minimum Frequency	Short v Med. Peeps	0.9	NS
	Short v Long Peeps	34.9	P<.005
	Med. v Long Peeps	24.7	P<.005
Energy	Short v Med. Peeps	2.4	NS
	Short v Long Peeps	132.7	P<.005
	Med. v Long Peeps	99.3	P<.005
Average Power	Short v Med. Peeps	5.9	NS
	Short v Long Peeps	196.0	P<.005
	Med. v Long Peeps	133.8	P<.005

Rate of peeping

The mean duration for successive calls between the beginning of one peep and the beginning of the next was established for each chick. Three short and three long peeps from each chick were used, and three medium peeps from five chicks and two medium peeps from the other two chicks were used. The mean rate of peeping for the short, medium and long peeps; = 1.99/sec., (SD = 0.9915); 1.13/sec., (SD = 0.911); 2.46/sec., (SD = 0.475) respectively. While the long peep is emitted at a faster rate than either the medium or the short peep, the difference in rate

between call types was not significant, (F= 0.46, N.S. between calls; F= 0.81, N.S. between chicks).

The stability of acoustic parameters

The similarity between peeps was examined using the Pearsons Product-Moment Correlation (r). Two successive short, medium and long peeps from each of the seven chicks were selected and compared. As can be seen from Table 4 there is a significant positive correlation for the short, medium and long peeps for duration. Ten of the sixteen correlations on the other six parameters are significant.

Table 4. Pearsons product-moment correlation coefficient (r) of the first and second peep calls for each call type (short, medium and long) (n=7 chicks).

Parameters	Call Type	r	P
Duration (ms)	Short Peep	0.83	P<.025
	Med. Peep	0.92	P<.005
	Long Peep	0.91	P<.005
Maximum freq.	Short Peep	0.65	NS
(kHz)	Med. Peep	0.99	P<.001
	Long Peep	-	-
Minimum freq.	Short Peep	0.89	P<.005
(kHz)	Med. Peep	0.70	P<.05
	Long Peep	0.99	P<.001
Difference between	Short Peep	0.55	NS
max. and min.	Med. Peep	0.90	P<.005
frequencies (kHz)	Long Peep	-	-
Peak frequency	Short Peep	0.73	P<.05
(kHz)	Med. Peep	0.57	NS
	Long Peep	0.96	P<.001
Energy (Watts)	Short Peep	0.65	NS
	Med. Peep	0.75	P<.05
	Long Peep	0.64	NS
Average Power	Short Peep	0.84	P<.01
(Joules)	Med. Peep	0.90	P<.005
	Long Peep	0.45	NS

Are calls discrete or continuous?

Both Andrew (1963, 1964) and Collias (1987) argue that on occasion the peep (distress call) and twitter (pleasure call) of the chick grade into each other to produce new calls i.e. the chevron call and the circumflex call. We attempted to investigate whether this was true for the three types of peep call described above. Therefore, the three types of peep could exist as either a discrete call sequence or as a sequence that changes from one call type to another in a given bout. Three different chicks moved from short to medium to long peeps in a short time period (see Figure 3). Reber (1985) defined the term discrete as "separate, distinct, individually identifiable and discontinuous" (p. 205), while a
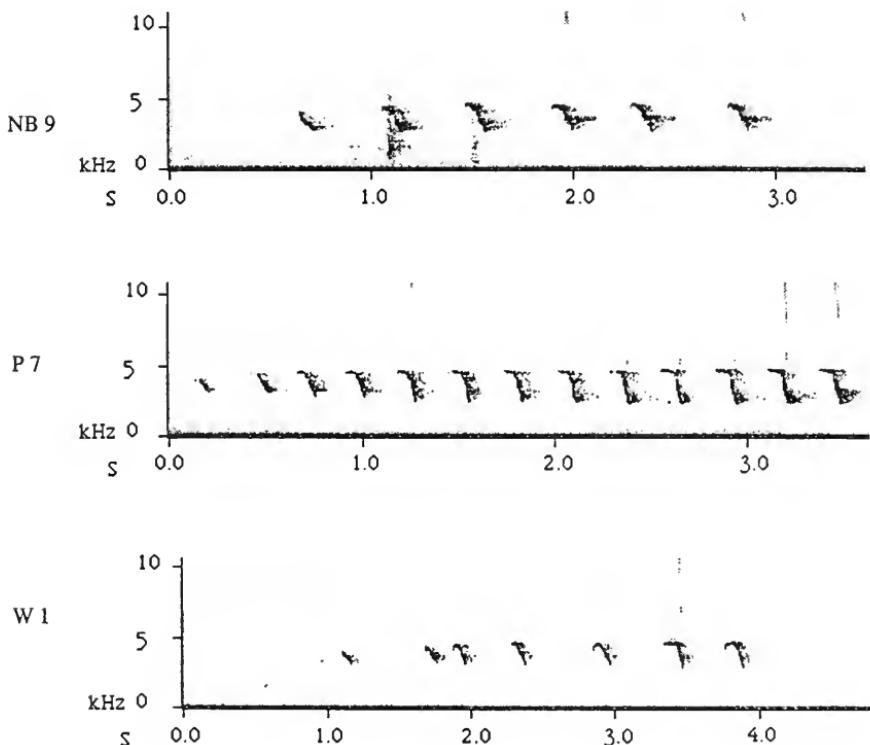
Figure 3. Spectrograms from three chicks of the three calls moving from short to medium to long (left to right). The identity of the chicks is located in the left hand margin. Only chick P7 produces the three call types in a single bout

continuum is defined as "any uninterrupted series of changes, any continuous gradually changing sequence of values" (p. 154).

The three peep types produced by one chick in a sequence of calling (see chick P7 Figure 3) are are the same as the calls that appear in individual bouts of calling (see Figure 2). Thus, these calls can change from short to medium to long in a single bout. The three peep types can be produced in discrete form and this is the most prevalent form of calling. In general it is also indicated that the chick pauses before changing from one type of peep call to another. However, it is evident that the three calls can also be produced in the same bout as illustrated in Figure 3 (chick P7).

DISCUSSION

The main finding of this study is the change in the structure of the peep vocalization during the 5 minute test period. The short peeps are similar to the short peep presented by Andrew (1964), the medium peep is similar to the distress call of Collias and Joos (1953) and the long peep is similar to the "Le cri d'appel du Poussin isolé" presented by Guyomarc'h (1962) (see Figure 2 and Wood-Gush, 1971, pp. 28-29). This study demonstrates that these three peep types can be produced by the same chick.

One of the underlying problems involved in the analysis was the distinction between discrete and continuous call types. All three call types have a similar basic structure in that they have descending frequencies. The three different calls show no significant differences in their peak frequency (see Table 2 (a)). The range measures for peak frequency show considerable overlap for the different call types (see Table 1) indicating that chicks tend to emphasise frequencies between 2.5-4.5 kHz for all call types. This shows that the different call types have a similar internal frequency-power structure. Second, these calls occur in the same context, i.e. there are no changes in the environment external to the animal during the recording session though the duration of the separation from cage mate increased over the 5 minute recording session. Other extraneous factors are unlikely to have influenced peep calling as the same heat lamps were used in the rearing and testing situation maintaining the temperature at a constant state. Thus, the calls have a similar basic physical structure and occur in the same experimental context.

Despite the similarity in basic structure, different forms of the call are evident, in visual inspection of spectrograms (see Figure 2) and in

statistical analysis of call parameters. Variation in the use of energy and average power indicates that there is a greater investment of energy in the calls as they move from short to long (see Tables 1, 2 (a), 3). A significant difference in duration exists for all three call types (Table 3). Significant differences exist between the short and long peep and between the medium and long peep for the parameters of minimum frequency, energy and average power (Table 3) and between maximum and minimum frequency (Table 2 (b)). Further, successive calls show a high degree of similarity evident by the statistical significance of 13 of 19 correlations performed on the seven parameters of the three peep types (Table 4).

However, range Figures (Table 1) for five of the seven parameters indicate that short and medium peeps overlap each other. These results suggest that a continuum may exist between short and medium peeps. Further, the coefficient of variation (c.v.) (Table 1) is lower for the long peep on all parameters except for minimum frequency. The greater variation (c.v.) in the short and medium peeps suggest that these two calls could merge into each other or develop from short to medium in a bout of calling. Under the current definition of a bout we are restricted to evidence from only one chick (see Figure 3, chick P7). However, an auditory inspection of the tapes and a visual inspection of the spectrograms (Figure 2) indicate that the three call types are distinct although differences between the long peep and the other two are more pronounced. This is further supported by a significant difference between the call types for the parameters of energy and average power in the statistical analysis. Different peep types can occur in the same bout although the calls maintain their distinctive physical structure as evident in Figure 3.

The Peep in context

Kaufman and Hinde (1961) found that isolated chicks in a strange pen produce distress calls (peeps) at a higher rate if the environmental temperature is lower than body temperature. Andrew (1964) focused on the twitter and has shown that with increased intensity of stimulus contrast associated with the presentation of food there is an increase in intensity of the twitters as shown by increased length , pitch and number of trilling cycles. In Andrew's (1964) study the chicks were presented with food which may be regarded as a positive stimulus. In this study the chicks were separated from a companion and such separation is associated with an increase in peep vocalizations (Collias, 1952; Kaufman and Hinde, 1961; Evans, 1975).

Bermant (1963) found that the rate and intensity of distress calling (peeping) increased with an increase in the degree of maternal isolation. Chicks that were alone emitted more distress call than chicks that could see and not hear the mother hen, who in turn emitted more peeps than chicks that could see and hear the mother hen. According to Collias (1987) and Collias and Joos (1953) distress calls (peeps) and pleasure notes (twitters) reflect the basic security-insecurity balance that governs chick behaviour. In the study of Bermant (1963) the chicks experienced graded levels of insecurity. Evidence from imprinting studies show that there is an increase in distress calling when a familiar imprinting object is removed (in chicks, Brown, 1979; in ducklings, Hoffman, 1968; Hoffman *et al.* 1974). The chicks' peeps affect the behaviour of the mother hen. Hughes *et al.* (1982) found that the sound of the chicks' peep vocalizations elicited approximately four times more food calling from mother hen than the sight of a silent chick. Evans (1975) points out the vocal interaction between hen and chick serves to maintain family unity.

The main finding of this study is that the same chick can produce three different types of peep call. These can be emitted in discrete bouts (see Figure 2) or in the same bout (see chick P7, Figure 3). The peep call is emitted in several situations. It occurs when a companion is removed (Bermant, 1963), when environmental conditions are not optimal (Kaufman and Hinde, 1961) and following the removal of a imprinting object (Brown, 1979). It also produces a specific reaction from the broody hen (Evans, 1978; Hughes *et al.*, 1982). The purpose of this paper was to examine in detail the three peep types of the chick. This was achieved by giving a detailed analysis of the three different peep types. Although the chick gives three types of peep call it is a matter for further investigation to determine if the different peeps perform separate functions and to determine what these functions are.

ACKNOWLEDGEMENTS

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SOME OF ARISTOTLE'S WRITINGS ABOUT BIRD BEHAVIOR AND ISSUES STILL CURRENT IN COMPARATIVE PSYCHOLOGY

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As is evident from the writings of Aristotle, Plutarch, and other classical authors, the ancients were already familiar with some of the salient features in the reproduction of birds. (Skutch; 1979: XVII).

ABSTRACT: In his search for the causes of the diversity observed in living beings, including humans (*zoa*), Aristotle did not define them by their bodily parts and generation process only. He also payed extensive attention to nutrition and especially to character (*ethos*). Indeed, combined with the other three types of features, it determines the way of life (*bios*) and subsequent activities (*praxeis*) of each species at both intra- and extra-specific levels. Character in the less developed and shorter-lived animals is less obvious. Conversely, the longer-lived ones are granted "a certain natural capability in relation to each of the soul's affections" (*HA* 608a11-13). Birds are of that kind. The present paper examines how birds are approached by Aristotle with respect to breeding and parental care in order to shed some light on the method, purpose and results of his comparative psychology.

INTRODUCTION

One of Aristotle's chief intents in what we call his zoological or biological writings was to determine the causes of "the main differentiating characteristics" (Lloyd, 1983: 18) of *zoa*, *i.e.* of all living beings including man. Indeed, these differences were reviewed with respect to such criteria as, first, faculties of sensation, means of locomotion, anatomical structure and morphology, methods of

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reproduction, etc., and, second *(HA* VII[VIII].1.588a18), activities *(praxeis)*, ways of life *(bioi)*, character or dispositions *(ethe)*. In Aristotle's view, the behavioral patterns were interdependent and clearly deserved as much attention as the physiological ones, although his approach is not to be identified with the modern science known as ethology (Labarrière, 1993). When he listed the activities of *zoa* *(HA* VII[VIII].12.596b20-24), he first mentioned the reproductive process (mating and the production of young); then the supply of food. They "engage" as he says, "the efforts and lives of all living beings" *(HA* VII[VIII].1.589a5-6). Third, he considered how they cope with the changes of seasons and temperature variations, which are indeed crucial to any being's survival and, consequently, its chances of reproducing.

The behavioral activities leading to the production of young are mainly addressed in *History of Animals* (literally: *Inquiries Concerning Animals),* books VII and VIII (in Balme's, 1991, revised numbering). For some species they are already reported in Book VI, which is devoted to the anatomical structures and physiological process of reproduction. Some further assessments are found in *Parts of Animals* and in *Generation of Animals* (to say nothing here of the so-called *Parva Naturalia).* In other words, mating and producing young are given extensive attention, as expected from their rank in Aristotle's scale of the activities of all living beings. However, his accounts are not developed to the same extent for each of them. For practical reasons, as he made clear, he could not know the ways of life of the insects and other lower animals to the same detailed degree as he did of higher beings *(HA* VIII[IX].1.608a11-13). It is currently accepted that he was "far better informed" about marine animals (see *e.g.* Balme, 1987a: 16) than about any other group. This may be true with respect to anatomical, morphological or physiological structures, although it still needs to be checked against the evidence on the terrestrial animals, especially birds and mammals. Yet whatever the method used to examine the different animals mentioned by Aristotle in each order of the animal kingdom (Balme, 1987a: 16; Lloyd, 1983: 37, n. 135; Louis, 1975: 101; Meyer, 1855: 144; Steier, 1913: 113; Sundevall, 1863: 23-24), birds came first with about 160 different species, groups or categories considered more or less extensively. They supplied him with the largest amount of data concerning reproduction.[1] Modern naturalists and especially bird watchers are not at all surprised by this. Birds behave less secretively

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[1] For an overview of Aristotle's contribution to ornithology see Streseman (1975: 3-7). Significantly enough, Labarrière (1993: 289) mainly relies upon Aristotle's account on birds.

than mammals when engaged in reproducing and appear more caring for their young than most fish and reptiles (to say nothing about the technical problems encountered to watch the reproductive behavior of these animals). Nevertheless, Aristotle's account of bird reproduction has not yet been thoroughly studied.

I shall attempt to outline some of the notable aspects of Aristotle's account, first, by surveying his report on the activities, ways of life, and character of birds with respect to the production of young; secondly, by examining two of his examples more closely; and thirdly, by looking at his purpose when considering the breeding behavior of birds, in order to reach some provisional conclusions. Before turning to the core of the matter, a few preliminary remarks need to be made.

PRELIMINARY REMARKS

Terminology

General terminology and "biological" writings. Derived from Greek terms, such words as "zoology," "biology," and "psychology" sound as if they had been coined by the ancient Greeks themselves. They are actually of much later origin. "Psychology" may be as recent as the 15th,[2] "zoology" as recent as the 16th, and "biology" as recent as the 19th century. Neither "zoology" ("scientific study of the animals") nor "psychology" ("scientific study of behavior and mental processes") was given its modern definition before the latter half of the 18th. Therefore, referring to Aristotle's "biological" writings or to Aristotle's "zoology" or "psychology" is done so for convenience.

"Genus" and "species". The terms "genus" and "species" have generated an impressive array of research due to their importance in Aristotle's writings (see *e.g.* Gotthelf, 1985: 17-128 [six papers on "Substance, Form and Species"]; Lennox, 1987; Pellegrin, 1986, 1987, 1989). These terms will be used here only when birds mentioned by Aristotle are identified with the corresponding categories in the Linnaean classification. For instance, *coccux = Cuculus canorus* (Grey cuckoo);

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[2] Boring (1966: 167) called attention to a paper by Krstić (1964) on Marco Marulić (1450-1524), author of a lost book entitled *Psichiologia de ratione animae humane* (*sic*). Unnoticed in *OED* and in *TLF*.

perdix = *Alectoris* gen. (Partridge).[3] Elsewhere, colloquial words such as "kind," "type," etc., are used.

Aristotle's "biological" writings

The authorship, chronology, general aims and sources of that part of the Aristotelian corpus, more than 25% of the whole, are still much debated. It is not appropriate to examine them at length here, but a few limited comments will be made.

Authorship and chronology. Regarding authorship, I follow David Balme (1991) and accept his arguments against those who claim that books VII and VIII (in Balme's numbering) of *History of Animals* are spurious. The period of Aristotle's life when he was supposed to have written his "biological" treatises is another puzzling issue that does not directly affect the present article. I refer the interested reader to the provocative arguments developed by Balme (1991: 1-13).

General aims and method. Taken as whole, Aristotle's "biological" writings were not designed to be an "animal encyclopaedia" (Balme, 1987a: 9; see also *e.g.* Lloyd, 1983, 1987). Neither should they be assimilated, when taken separately, "to the present-day categories, classifying the *HA* as natural history, the *PA* as comparative anatomy, the *PN* as physiology, the *GA* as embryology." They are rather to be considered (Balme, 1987a: 11) as "studies of ... philosophical concepts ... made through empirical data" on *zoa*. Indeed, they address similar problems to those under examination in the writings on logic and metaphysics and focus upon what may be learned from living beings and their "biological" processes about substance, form, species, essence, *logos.*

Sources. The origin of Aristotle's information in his "biological writings" is another much discussed issue referring to the interrelated questions of his method and of the reliability of his work. Three main categories of sources used by Aristotle are recognised by modern commentators. First, Aristotle obtained data from former or contemporary writers (regardless of their own aims and specialities). He identified the authors he criticized more often than he did those he agreed with, although he is not as spiteful towards his predecessors as claimed by Byl (1980). As a result, the identity of all the authors of his written sources may not be fully ascertained.

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[3] Thompson (1936) remains the reference book on ancient Greek evidence about birds, although it is now out of date in some respects and needs updating.

Second, Aristotle relied upon information provided by animal specialists such as hunters, fowlers, fishermen, farmers and breeders, etc., and, especially with respect to birds, by occasional watchers and owners. The importance of the latter should not be underestimated. Indeed, birds played a prominent role in the lives of people from the earliest times and thereafter (Keller, 1913; Pollard, 1977). Countless sources of evidence of many kinds (see, for instance, Böhr, 1992; Spyropoulos-Vanderpool, 1985) confirm that the Greeks were fond of birds and rather well informed about them (for various reasons or purposes). Aristotle referred to this category of his sources anonymously. He introduced their reports by such sentences as: "The experts declare" (*HA* VIII[IX].8.614a19); "It is commonly reported" (*HA* VIII[IX].13.615b24); "Some say" (*HA* VIII[IX].13.615b24-25); "So they say" (*HA* VIII[IX].15.616b7); "Others say" (*HA* VIII[IX].29.618a16); "They say" (*HA* VIII[IX].32.619a8); etc. Depending on the opinion proffered, he included their data in his account as further examples, or argued against them, or took them as starting points for his own comments.

Last, and certainly important, his third source comprised his own observations, some of which were based upon experimental programmes carried out by himself or others in his circle of influence (for example, egg development: *HA* VI.3.561a4 - 562a22; and probably bird song: *HA* IV.9.536b14-17; etc.).

OVERVIEW OF BIRD BREEDING

Had Aristotle given his own definition of parental care in birds, he likely would not have agreed with the restricted definition of some modern scientists who limit parental care to the activities displayed by parents after egg hatching. Aristotle's evidence on breeding behavior in birds involved all stages of the process of bird reproduction (Skutch, 1979). For the sake of clarity, they are listed in Table 1. Such were the main points Aristotle touched upon or developed to some extent, referring to the rich avifauna of the East Mediterranean area (Kanellis, 1969).

Table 1. A selection of Aristotle's evidence on breeding behavior in birds.

Behavioral stages	Bird species	Reference
nesting season, formation of pairs and stability	pigeon	*HA* VI.1.558b13; VIII(IX).7.612b32-34; etc.
nest sites	partridge, quail and the like	*HA* VIII(IX).8.613b6-12
	eagle	*Ha* VIII(IX).32.619a25-28
nest building	swallow	*HA* VIII(IX).7.612b23-28
courtship	pigeon	*HA* VI.2.560b25-30
female reactions after mating	hen, pigeon or goose	*HA* VI.2.560b7-11
egg laying & clutch size	partridge	*HA* VIII(IX).8.613b22-23
sitting period	pigeons (female and male taking turns)	*HA* VI.4.562b18-19
	goose or bustard	*Ha* VI.6.563a28-29
hatching	pigeon	*HA* VI.4.562b19-21
brooding and temperature regulation	pigeon	*HA* VI.4.562b21-23
nest sanitation	swallow	*HA* VIII(IX).7.612b29-32
feeding	pigeon	*HA* VIII(IX).7.613a3-6
defending the nestlings directly:	passerines	*HA* VIII(IX).29.618a30-31
	eagle	*HA* VIII(IX).32.619a23-25
by stratagems:	partridge	*HA* VIII(IX).8.613b18-22
teaching the nestlings how to feed	partridge	*HA* VIII(IX).8.613b12-13
	eagle	*HA* VIII(IX).32.619a20-23
teaching the nestlings how to fly when fully-fledged	"black eagle"[4]	*HA* VIII(IX).32.618b29
teaching how to sing	song-birds	*HA* IV.9.536b14-19

The accuracy of many of Aristotle's data on bird behavior (as well as on anatomy, morphology, and physiology) has been confirmed in

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[4] Considering Aristotle's data, Pollard (1977: 77) tentatively identifies the "black eagle" with Bonelli's eagle (*Hieraaëtus fasciatus*). See also Thompson, (1936: 2-3).

modern times.[5] Conversely, he has been shown to be wrong on some other points (for instance, on duration of incubation, see Peck, 1970: 246-247), for reasons which themselves need further investigation. They are likely to be linked to his theoretical prejudices such as on the pairs "right, left," "male, female," etc. (Lloyd, 1991) or his philosophical convictions, for instance on the still much discussed issue of natural teleology (Balme, 1987; Cooper, 1987; Gotthelf, 1987).

Here, it will be enough to emphasize that Aristotle considered both wild and domestic birds. The remoteness of some species (for instance, vultures: *HA* VIII[IX].11.615a13-14, or eagles: *HA* VIII[IX].32.619a25-27) did not prevent him from gathering first-hand information on their breeding habits. However, the largest amount of reliable information concerns birds that were most familiar to the Greeks, either because they were domestic species (cocks and hens, etc.) or because they were reared, or tamed, like partridges and quail (Pollard, 1977: 105-109), or were kept as singing birds (Pollard, 1977: 135-40).

Most of Aristotle's descriptions of bird reproduction were listed (even in *HA* VI) as further examples of the differences being investigated in all kinds of living beings. They generally point out one feature or another. They are sometimes repeated with or without additional details or, worse, with apparent discrepancies (for example, concerning the hoopoe's nest, compare *HA* VI.1.559a8-11 and VIII[IX].15.616a37 - b1). The way he arranged the data also refers to the organization of the biological treatises. It does not always provide easy and reliable access to Aristotle's thinking, a problem exacerbated by his defining few, if any, of his key-terms. Nevertheless, clues can be found that shed some light on the concepts underlying his approach to the reproductive behavior of birds.

CLOSER EXAMINATION OF TWO EXAMPLES

Brood parasitism of Cuckoo

The brood parasitism of the Grey cuckoo (*Cuculus canorus*) is one of the compelling issues in bird breeding. As is well known, European cuckoos do not build nests. After mating the female selects the nest of

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[5] For instance, on partridges see Johnsgard (1988:114-118); on pigeons, Cramp-Simmons, IV (1985: 288-298), Grüll (1980: 25-42), and Vindevogel *et al.* (1987: 108-112); on eagles, Brown-Amadon; and on bird song, Armstrong (1973), Hartshorne (1992), and Thorpe (1961).

another bird, nearly always a song-bird of the species which had raised her. She makes her choice of the nest at the time when the host female has started laying. The cuckoo female picks up one egg (which she will throw away or swallow) from the host's clutch and lays her own. Her egg usually hatches before the eggs of the host, and her nestling shoves them out, reducing the breeding success of the host. Indeed, only the young cuckoo is likely to survive, and it is cared for by the host or foster parents (Wyllie, 1981).

Aristotle described the cuckoo's reproductive process, in comparison to that of other animals, at some length (*HA* VI.7.563b29-564a3; VIII[IX].29.618a8-31; *GA* III.1.750a12-16). However, he obviously did not have an extensive knowledge of what happens to the eggs or nestlings of the host species and the circumstances and causes of egg destruction or of host-nestlings' starvation (Bodson, 1982). Aristotle reported three hypotheses conveyed by common opinion (introduced by: "so they say"), based upon "people's own watching" (see above). He did not suggest which hypothesis should be accepted, and he concluded by saying (VIII[IX].29.618a26-31; Balme's translation):

> It seems that the cuckoo manages its reproduction intelligently (*phronimon*): for because it is conscious of its own cowardice and inability to give help, for this reason it makes its own chicks supposititious, as it were, in order to save them. For this bird is exceptionally cowardly: it has feathers plucked by the little birds and runs away from them.

Modern ornithologists still discuss the origin and adaptation of the cuckoo's brood parasitism. They confirm that the cuckoo female is attacked by the smaller birds (passerines) whose nests she parasitizes, but ornithologists refrain from describing her as being cowardly. In Aristotle's biological works, such words as "cowardly," "courageous," "gentle," "aggressive," "scheming," "fawning," "jealous," etc., are commonly used (Bertier, 1993). They did not originate from popular belief as was once admitted by Lloyd (1983: 24; 1984).[6] These terms did not retain their anthropomorphic meaning either. Being transposed from man and his distinctive scale of values to other animals, they lost their ethical connotations and simply relate to natural behaviors and reactions (Fortenbaugh, 1971: 67-70; Labarrière, 1990: 415; Lloyd, 1983: 25).

Deemed more important here is the intelligence (*phronesis*) attributed by Aristotle to the cuckoo. *Phronesis*, precisely "practical intelligence," is the criterion in *GA* III.2.753a8-17 by which he classifies the *zoa* with respect to their intimacy and attachment to their offspring.

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[6] Criticized by Labarrière, 1993 and Lennox, 1985.

There the class of birds (taken as a whole) is listed in second position, after human beings and some other mammals. The latter, which "have more practical intelligence (*phronimoteron*), ... which are endowed with most practical intelligence (*phroneseos*), show intimacy and attachment towards their offspring even after they have reached their perfect development". Birds "show it –only– until they have produced their chicks and brought them up". Remarkably enough, the cuckoo, managing its offspring as it does, is said to be no less intelligent than swallows, pigeons, partridges, etc., all birds actively caring for their own nestlings. Indeed its *phronesis* is deemed to make the cuckoo conscious of its cowardice and capable of reaching the supreme aim of reproduction: survival of the offspring.

The origin of the swallow's art of nest building

Aristotle opens (chapter 7) his extensive review *(HA* VIII[IX]) on animal ways of life with the case of the swallow. He first mentions the process of nest building *(HA* VIII[IX].7.612b23-28; slightly modified from Balme's, 1991, translation):

> In the mixing of straw into mud she keeps the same order.
> She interweaves mud with the stalks, and if she lacks mud,
> she moistens herself and rolls her feathers into the dust.
> Further she builds the nest just as humans build, putting the
> stiff materials underneath first, and making it match herself in
> size.

Despite Thompson's (1936: 316) statement, Aristotle does not provide such details as those mentioned by other ancient authors[7] (for instance, Theocritus, *Idylls* 14.39; Vergilius, *Georgica* IV.307, as cited in Arnott, 1967); Theaetetus Scholasticus, in *AP* X.16.5-6) that clearly differentiate the House Martin (*Delichon urbica*) from the Barn Swallow (*Hirundo rustica*). Both species build a cup-shaped nest of mud (Goodfellow, 1983, Ch. 7; Hund-Prinzinger, 1985: 484-487; Suter, 1985: 310-311, Fig. 52, 410-423; Turner-Rose, 1989: 26-27, pl. 15 and 24), although what Aristotle said of making mud (moistening themselves and rolling their feathers in the dust) has not been confirmed and is

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[7] This statement by Pollard (1977: 30), is ambiguous: "The Ancients did not distinguish the swallow (*hirundo rustica* [*sic*]) from either the house martin (*delichon urbica* [*sic*]) or sand martin (*riparia riparia* [*sic*])." He should have added "in their naming". Their descriptions, especially on the nesting site, confirm that they did not confuse the species with one another.

indeed questionable.[8]   Nests differ from one another only by their position, attached to a roof or a beam: *Hirundo rustica* or close up beneath the eaves, *Delichon urbica,* and the size of entrance: largely open in *H. rustica*, a small entrance hole in *D. urbica*. Whether Aristotle refers to the former or the latter species does not matter too much here, but how he comes to his assessment on swallow's nest building is worth considering.   Indeed, having stated at some length (chapters 1-6) the differences observed mainly in mammals' behavior and character, he turned to the ways of life of other animals introducing the point as follows (*HA* VIII[IX].7.612b18-23; adapted translation, after Balme, 1991:

> In general, with regard to their lives, one may observe many imitations of human life in the other animals, and more especially in the smaller than in the larger animals one may see the precision of their discriminating intelligence (*dianoia*): for example, first in the case of the birds, the swallow's nest-building.

As in the case of the grey cuckoo, intelligence is mentioned to justify a pattern of behavior that is commonly admired. Yet the concept of "intelligence" is not referred to with the same word as that applied to the grey cuckoo. Swallows are granted *dianoia*: "analytical intelligence" or "discriminating intelligence". Aristotle was much interested in non-human intelligence, and he scrutinized the activities and conduct of many animals with respect to the smaller or larger share in different types or degrees of "intelligence" which they display. The problem is that he did not provide an explicit definition of such types or degrees. As was recently shown by Labarrière(1990), Aristotle differentiated between qualities, stages, or levels of intelligence by purposely varying his vocabulary. When preferring *dianoia*, the type of intelligence he identified in the swallow's nest building process, he used one of the words he also (though not exclusively) applied to human intelligence. This does not mean that he mistook the bird's intelligence for the human's, but that he perceived that the ability displayed by a swallow in selecting and using its materials so efficiently results from some skill superior to a merely "practical" intelligence. He viewed the swallow's action as being related to the human discernment or analytical intelligence closely enough to be called *dianoia* and not *phronesis*. His choice was all the more meaningful since what is eventually achieved by

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[8] I am most grateful to Dr. A Demaret for his helpful information and comments on this particular point.

the swallow's art of nest building is indeed a "practical" or "material" piece of work.

For all its interesting characteristics, the swallow's art of nest building is not the only activity noted by Aristotle about that bird. He also emphasized other traits of its discriminative aptitude such as feeding the nestlings and teaching them nest sanitation.[9] Furthermore, the swallow's way of life is only the first of the examples Aristotle reviewed in *HA* VIII(IX). Regarding birds (before he turned to fish, insects, and mammals), he described, for example, the monogamous habits of pigeons and the stratagems of partridges saving their nestlings from the hunter. These provided him with resemblances (Fortenbaugh, 1971: 152; Thompson, 1910) or parallels (Pollard, 1977: 19) –*mimemata*– between the human way of life and the *bioi* of the other living species, namely the animals.[10]

PURPOSE

Assessing the final aim or teleology of nature in whatever is achieved is one of the main features of Aristotle's system, although his definition of final causality has not been found in what is preserved of his work (Gotthelf, 1987: 204). His statement about the cuckoo's reproductive behavior –"in order to save the chicks"– explicitly refers to the final aim. It is only implicit in the swallow's process of nest building as characterized in *HA* (see above), but it is firmly emphasized in the extensive demonstration of natural determinism in *Physics* II.199a21-30 (Balme, 1987b; Cooper, 1987), where "the swallow making her nest" is taken as a meaningful example. Nevertheless, when describing reproductive behavior and parental care in birds (and other animals), Aristotle seemed to have been more interested in the animal's

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[9] Labarrière (1993: 293) says that swallows are mentioned as first examples of the category of birds "easily finding their food" (*eubiotoi*) and "kind to their young" (*euteknoi*). For such terms, see (for instance) *HA* VIII(IX).11.614b31-34 (*euteknoi*), 15.616b10 (*eubiotos*). Indeed, swallows relate to both classes with respect to their breeding behavior. However they are explicitly given those qualifications nowhere in the biological treatises. Even in 612b18-22. Aristotle refers to swallows neither as *euteknoi* nor as *eubiotoi*, but for their paradigmatic *dianoia*. See next paragraph.

[10] Cole (1990: 53, n. 18, unchanged from the 1st edition), after Sikes (1914: 61-62), states that in Aristotle's view, "birds learned to build nests in imitating human dwellings." Bertier (1994: 488, n. 2) has the same, although apparently independent from Sikes and Cole, misinterpretation (which involves Democritus, 68 B 154 Diel⁶-Kranz. See Bodson, 1996).

intelligence and cognitive faculties (Dierauer, 1977; Sorabji, 1993) than in anything else. Indeed, the topic involves further comparisons between all living beings, not so much between birds and birds or mammals or insects as between humans and other animals. Intelligence was a key issue in Aristotle's logical classification (Pellegrin, 1987) with humans at the top of the hierarchy (Lloyd, 1983: 26-42).

CONCLUSION

The aim of this survey was to outline the Aristotelian evidence on the breeding process and parental care in birds. The first provisional conclusion is that the amount and diversity of data gathered on such matters in the biological treatises is fairly impressive, in both extent and general accuracy, although this needs further investigation. Meanwhile, Aristotle's research on birds appears to be rooted in the ancient Greeks' cultural interest in those animals and in his own attention to them. It led him to conduct or to instigate observations and experiments, the accuracy of which remains astonishing in some cases. As to his comparative psychology, when dealing with bird breeding, it appears, not surprisingly, to refer repeatedly to human features. The fact is consistent with Aristotle's main purpose, and it enabled him at the same time to provide the European tradition of ornithology with a masterful opening.

ACKNOWLEDGEMENTS

ABBREVIATIONS

AP = *Anthologia Graeca*
GA = *Generation of Animals*
HA= *History of Animals*
OED = *Oxford English Dictionary*
PA = *Parts of Animals*
PN = *Parva Naturalia*
TLF = *Trésor de la langue française*

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CURRENT ISSUES IN COMPARATIVE PSYCHOLOGY

RECOGNITION OF HUMANS BY ANIMALS

Editorial Comments

Many "higher" animals are commonly assumed to distinguish between individual humans. This belief is based largely on anecdotal reports. In reality, there is little empirical evidence to support human recognition in non-human species. In the following paper Taylor and Davis report evidence that llamas can recognize individual humans. Although the data are preliminary, they suggest an important cognitive ability in a species whose behavior remains largely unexplored. Moreover, they raise the issue of the possible influence of familiar versus strange handlers on research and on animal management in zoological gardens or on farms. We hope that this preliminary set of observations will stimulate further discussion about the possibility of human recognition by animals. In order to evolve a comparative psychology of human recognition, Taylor and Davis would like readers to share similar evidence, especially in cases involving relatively uncommon species. Studies involving so-called "lower" species (invertebrates, reptiles, amphibians) would be of particular interest.

THE RESPONSE OF LLAMAS (*LAMA GLAMA*) TO FAMILIAR AND UNFAMILIAR HUMANS

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ABSTRACT: The current study explored the response of llamas to familiar and unfamiliar humans under housing and management conditions typical of both zoological gardens and llama farms. A group of five adult llamas was exposed to three 30-min socialization sessions with one female handler, who offered food and tactile contact. Subjects were then tested for their responses to the familiar handler (A) versus a stranger (B) in an A_1-B-A_2 design. Proximity to the handler, sampled at 5-sec intervals through the 1-min test exposures, was used as a dependent variable. For both the A_1-B and B-A_2 comparisons, the number of animals present in the test area was significantly lower in the presence of the unfamiliar human ($p < 0.001$; 2-tailed Randomization Test). This finding has important implications for llama housing and management, where individual humans may serve as discrete conditioned or discriminative stimuli if repeatedly paired with hedonic events. Such human-based conditioning may affect animal behavior, physiology, and motivation. Interactions with humans may thus potentially confound experimental results in a research environment, or be used to facilitate management or training.

The llama (*Lama glama*) and its smaller relatives, the alpaca and vicuña, have been domesticated for nearly 5,000 years. Traditionally prized in Peru for their meat and as beasts of burden, llamas were first reintroduced to the United States in the late 1800s. Until recently, North American llamas have been housed principally in zoological gardens or exotic animal farms. Since the 1970s, llamas have been increasingly kept in Canada and the United States as pack animals, flock guardians, and companion animals.

The llama's usefulness as a work or companion animal depends on the success of close contact with humans. Whereas the effects of human-animal interactions on the human participants are typically well documented (e.g., Boldt and Dellman-Jenkins, 1992; Loughlin and Dowrick, 1993), the impact on the animals has been largely overlooked.

Nevertheless, it is hard to imagine that animals are unaffected by repeated interactions with humans. Whether positive or negative, these effects may have important implications for animal use in a variety of contexts. They may confound experimental results (Davis and Balfour, 1992) or be used to facilitate management or training (Pepperberg, 1992; Reinhardt, 1992).

Such human-based behavioral or motivational effects have a solid theoretical grounding in the psychological literature. Pavlov (1927) described the inevitable results of an animal's interactions with a scientist as a "socialization reflex". Because human caretakers or experimenters are frequently associated with hedonic stimuli (e.g., food, pain), they readily come to predict the arrival of such events (Morton, 1990). Gantt, Newton, Foyer, and Stevens (1966) have documented and described this process in terms of "Person as CS" (Conditioned Stimulus). Human-animal interactions may also be understood in terms of operant conditioning. For example, Taylor and Davis (in press) have reported evidence of cattle using individual humans as discriminative stimuli for positively reinforced operant responding. Whether scientist-animal interactions are described in Pavlovian or operant terms, the fact remains that their effects are directly measurable. Indeed, Davis and Balfour (1992) provided wide-ranging evidence of the impact of interactions with humans on the behavior and physiology of animal subjects.

The implicit assumption underlying such observations is that animals can discriminate between individual humans in their environment. To date, evidence of human discrimination by animals is primarily based on anecdotal reports by pet owners, zookeepers, and livestock managers, and is intuitively confined to so-called "higher animals" (e.g., Hediger, 1964 pp. 162-163). Although there is little empirical evidence for this ability in any species, there are some exceptions. Slobodchikoff, Kiriazis, Fischer, and Creef (1991) report that prairie dogs emit alarm calls that are specific to individual human predators. Evidence suggesting human recognition has also been reported in dogs (Settle, Sommerville, McCormick, and Broom, 1994), chimpanzees (Boysen and Berntson, 1986), sea lions (Schusterman, Gisiner, and Hanggi, 1992), pigs (Tanida, Miura, Tanaka, and Yoshimoto, 1995), and rats (Davis, Taylor, and Norris, 1977).

Despite their long history of domestication and service to humans world-wide, llamas have been the subject of very little behavioral research. Although excellent training manuals and field reports of wild camelids exist, there appears to be no systematic information on the mechanisms underlying lamoid social behavior (e.g., Hoffman and Asmus, 1989; McGee and Tellington-Jones, 1992; Vilá, 1992).

Anecdotal reports suggest that llamas are curious, yet aloof, animals (Brillig Hill, Inc., 1995). Further, they appear shy and resent close physical contact with strangers (Franklin, 1984; McGee, 1994). Llamas are reported to recognize their regular caretakers or trainers (even after a period of separation), and to visually track known humans in a group of strangers (B. Russell, personal communication). To date, however, human-llama interactions have not been the subject of systematic research. Thus, the current study seeks to explore the response of llamas to familiar and unfamiliar humans under housing and management conditions typical of both zoological gardens and llama farms.

METHOD

Subjects

Five llamas (4 females and 1 male), ranging in age from 1 to 5 years served as subjects. The animals were housed in an L-shaped outdoor enclosure measuring approximately 9m by 9m (Figure 1). Subjects were fed a maintenance ration of mixed hay and ruminant cubes.
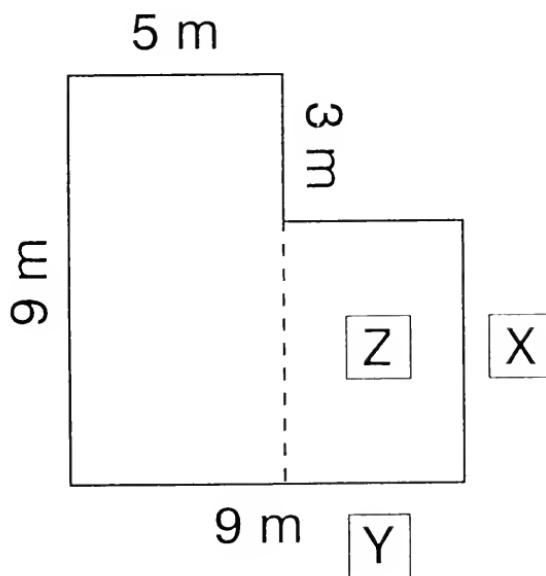

Figure 1. The experimental enclosure. X represents the location of the handler, Y is the location from which the test sessions were videotaped, and Z is the test area.

Procedure

Subjects were exposed to one female handler (AAT: Caucasian, 1.8 m) for three 30-min socialization sessions on successive days. The subjects had never seen this handler prior to the initial socialization session. During these sessions, the handler stood outside the enclosure at location X (Figure 1) and offered food rewards of ruminant cubes to animals who approached. Subjects who initiated physical contact with the handler were stroked gently on the neck. The handler spoke quietly to the animals throughout the socialization sessions.

On the fourth day, subjects were tested for their responses to the familiar handler versus a female stranger (Caucasian, 1.65 m). The test sessions consisted of successive 1-min exposures to the familiar handler (A) and the stranger (B) in an A_1-B-A_2 design. Exposures were separated by approximately 15 min. A test was not started until all animals were outside of area Z (Figure 1). To initiate a test exposure, the handler emerged from the adjoining barn and walked quietly to location X, where she stood motionless with empty hands outstretched (palms up) and resting on the top rail of the fence. All test sessions were videotaped from location Y.

Data Analysis

Preliminary observations revealed that physical contact with the handler was frequently affected by the social hierarchy within the group. The dominant animal would typically position itself close to the handler, effectively preventing the other animals from approaching. Thus, individual animal latency to contact the handler proved an ineffective dependent variable.

Instead, proximity was used as a behavioral indicator of recognition. At 5-sec intervals throughout the 1 min test exposures, the number of animals present in the test area was counted (see Figure 1, area Z).

The Randomization Test for matched pairs (Seigel, 1956) was used to evaluate the number of animals in the test area in the presence of the two humans. The Randomization Test was performed twice: once to compare the A_1 and B exposures; and then to compare the B and A_2 exposures. In each case, the numbers of animals present in area Z at each 5-sec interval were paired for comparison.

RESULTS

Table 1 reports the average number of llamas in the test area during exposure to the familiar and unfamiliar humans. These data suggest a general decline in the number of animals in the presence of the unfamiliar human. A statistical comparison of these data for each 5-sec interval of the 1-min test exposure confirms a significant difference in the llamas' response to the familiar and unfamiliar humans in both A_1-B and B-A_2 comparisons (p ≤ 0.001; 2-tailed Randomization test, Seigel, 1956).

Table 1. Number of llamas (maximum = 5) in the test area in the presence of familiar and unfamiliar humans during 1-min test sessions (average of 12 5-sec sampling intervals).

	Mean number llamas present per 5-sec interval
A_1 - Familiar	3.00
B - Unfamiliar	0.58
A_2 - Familiar	2.60

DISCUSSION

Our results support anecdotal reports that llamas can discriminate familiar from unfamiliar humans. Further, they manifest this discrimination by avoiding the unfamiliar handler (relative to the familiar handler) in an open-field test situation. This "avoidance" may, in fact reflect one, or both, of two distinct motivational mechanisms: a specific aversion to the unfamiliar handler (neophobia), or a relative lack of motivation to approach a handler who was never previously paired with positive hedonic stimuli. Given previous descriptions of the llama's wary nature (Franklin, 1984; McGee, 1994), an explanation in terms of neophobia seems most likely. In the present case, however, it should be stressed that "familiarity" with Handler A was facilitated by food, positive tactile stimuli, and a lack of threatening behavior. Whether such motivation is essentially appetitive or aversive (or, for that matter, reflects operant or Pavlovian conditioning), the fact remains that llamas readily discriminate between human handlers.

Our data do not allow us to identify the sensory modality used by llamas to make this discrimination. Given the distance (approximately 4 m) at which recognition was expressed, it appears likely that vision, rather than olfaction, was employed (B. Russell, personal

communication).   However, this conclusion is far from definitive. Virtually nothing appears to be known about the relative dominance of visual, olfactory, and auditory mechanisms in llama social behavior in general, or conspecific (or other) recognition in particular.

The finding that llamas can discriminate individual humans has important implications for their housing and management, both in zoological gardens and as companion animals. Once individual humans have been identified, they may serve as discrete conditioned stimuli (CSs) if repeatedly paired with the hedonic events that are fundamental to zoo or farm life. Such human-based Pavlovian conditioning may interfere with routine care and management if changes in personnel occur (e.g., weekend staff). In addition, llamas may be expected to distinguish humans who have performed aversive procedures in the past, making future interactions more difficult if appropriate training and/or desensitization is not performed.

On the other hand, positive human-animal interactions may be used to facilitate the management and training of llamas (McGee, 1994). Indeed, other species have been motivated to perform both simple and complex tasks as a result of close relationships with individual handlers (e.g. Boysen, 1992; Davis and Perusse, 1988; Pepperberg, 1992). Alternatively, animals have been trained to tolerate and willingly participate in potentially aversive management routines through the use of positive interactions with specific humans (e.g., Reinhardt, 1992).

Regardless of the nature of their effects, it is clear that repeated interactions with humans can have direct implications for animal behavior, physiology, and motivation (Davis and Balfour, 1992). Our findings confirm anecdotal evidence that llamas can discriminate individual humans, and that they respond negatively to the presence of strangers.   Such human-based effects should be considered when designing research protocols, scheduling personnel, and developing management and training programs for llamas.

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